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RESEARCH ARTICLE

Flicker-induced eye movements and the behavioural temporal cut-off frequency in a nocturnal spider

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SUMMARY

We investigated changes in the eye muscle activity in the spider *Cupiennius salei* as a response to temporal intensity modulations. These spiders are known to enhance eye muscle activity in their principal eyes when moving stimuli are detected in the secondary eyes. We measured the activity of the dorsal eye muscle using a small telemetric unit attached to the spiders' prosoma and confronted the animals to flicker stimuli presented on a cathode ray tube monitor. We registered a significant increase in eye muscle activity as response to temporal light intensity modulations, which implies that no directed motion is required to trigger the spiders' response. This allowed the determination of the behavioural temporal cut-off frequency. None of the frequencies higher than 8.6 cycles s^{-1} and all of the frequencies lower than 4.3 cycles s^{-1} elicited a significant increase in eye muscle activity. A behavioural cut-off frequency of only a few cycles per second is well in line with the temporal properties of the photoreceptor cells determined using intracellular recordings. A relatively low temporal resolution and a relatively high spatial resolution suit well *C. salei*'s lifestyle as a nocturnal sit-and-wait hunter.

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Key words: electrophysiology, eye muscle, spider eye, temporal resolution.

INTRODUCTION

Cupiennius salei (Ctenidae) retreats during the daytime and starts to hunt and search for mates at dusk (Barth and Seyfarth, 1979; Seyfarth, 1980). The spider is a sit-and-wait hunter (Melchers, 1967; Barth and Seyfarth, 1979) and is extremely polyphagous (Nentwig, 1986). Its mechanosensory systems are well developed and the spiders are able to catch flying or crawling prey without any visual input (Melchers, 1967; Barth and Seyfarth, 1979; Hergenröder and Barth, 1983). Pre-copulatory behaviour involves chemical and vibrational communication and no evidence for visual signalling has been found (Barth, 1993). Therefore, vision is often assumed to play a minor role, if any, in prey capture and mating behaviour.

However, in spite of the spider's nocturnal lifestyle and its impressive mechanical senses, the visual system is also astoundingly well developed. *Cupiennius* has, like most spiders, eight camera-type eyes. The two anterior median eyes (AME), which are also referred to as principal eyes, are each equipped with a dorsal and a ventral eye muscle that can move the retina (Kaps and Schmid, 1996). The three other eye pairs, the posterior median eyes (PME), posterior lateral eyes (PLE) and anterior lateral eyes (ALE), are referred to as secondary eyes. The photoreceptors in those eyes are arranged in rows within light-reflecting tapeta and the interreceptor angles along such rows are smaller than normal to it. Land and Barth (Land and Barth, 1992) investigated the eyes of *C. salei* and found that the lenses produce images of good quality on the retina. The smallest interreceptor angles are approximately 0.9–1 deg and were measured in the PME and PLE along tapetal rows (Land and Barth, 1992). This implies a spatial resolution that can challenge typical diurnal insects.

The eyes have also been found to be extremely light sensitive: electroretinogram (ERG) measurements suggested an absolute corneal illuminance threshold for white light of 0.0001–0.001 lx, which was 1–2 log units below 0.01 lx, the lowest intensity that could be measured with the luxmeter used (Barth et al., 1993). These results were confirmed by a more recent study using intracellular recordings (Pirhofer-Walzl et al., 2007). The photoreceptors' spectral range, peaking at 500–550 nm, drops to zero for wavelengths larger than 700 nm (Barth et al., 1993) and light sensitivity should thus be even better for light conditions encountered in the animals' natural habitat than measured for white light. The photoreceptor membrane in all eyes is subject to a substantial turnover (Grusch et al., 1997). The rhabdomeral microvilli are degraded at dawn and rebuilt at dusk; during night-time the microvillar surface is 10 times larger than during the day (Grusch et al., 1997). ERG measurements revealed a concomitant 10-fold increase in sensitivity at the spiders' night state for the AME, whereas, interestingly, no increase in sensitivity could be found for the PME (Barth et al., 1993). This might be compared with studies on the eyes of *Dinopis*: the PME clearly exhibit a daily membrane turnover (Blest, 1978), but no obvious increase in sensitivity at the spiders' night state could be revealed using ERG measurements (Laughlin et al., 1980).

The morphological and physiological properties of the eye muscles in *C. salei* were described by Kaps and Schmid (Kaps and Schmid, 1996). The eyecup can be deflected either by the dorsal muscle alone (resulting in microsaccades of approximately 3 deg amplitude) or by both the dorsal and the ventral muscle (resulting in longer excursions of 4–15 deg). The counteracting force to the muscle contractions is presumably the elasticity of the tissues. The authors found a clear correlation between the muscle potential

frequency and the deflection of the AME retinae (Kaps and Schmid, 1996).

The elaborate visual system and the importance of the visual centres in the brain (Strausfeld and Barth, 1993; Strausfeld et al., 1993) suggested the significance of the visual sense for these nocturnal spiders, which has been confirmed in several behavioural studies. For example, Schmid (Schmid, 1998) showed that *C. salei* approaches appropriate visual targets; thus, using twofold choice experiments, the different functions of the two sets of eyes could be investigated. The spiders are able to detect visual targets using either the secondary or the principal eyes, but for object discrimination, input from the principal eyes is required (Schmid, 1998). The spiders respond to movement presented in the visual field of the secondary eyes with an increase in eye muscle activity in the principal eyes (Neuhofer et al., 2009). Thus, the secondary eyes seem to be responsible for movement detection whereas the principal eyes are necessary for object discrimination (Neuhofer et al., 2009). The motion-detecting system was very recently shown to be colour blind (Orlando and Schmid, 2011). The field of view of the AME is shifted during locomotion; the spiders enhance eye muscle activity in the ipsilateral eye before turning and thus look in the subsequent walking direction (Schmid and Trischler, 2011). Visual stimulation alone is sufficient to release attack behaviour and this strongly suggests that the spiders are able to use visual cues in the context of hunting behaviour (Fenk et al., 2010b).

To test the spiders' spatial cut-off frequency, we recorded the increase of the eye muscle activity in response to moving gratings at different wavelengths (Fenk and Schmid, 2010). The difference between the interreceptor angles along tapetal rows and the interreceptor angles normal to the rows implies an orientation-dependent retinal resolution (Land and Barth, 1992). Our data indeed revealed an orientation-dependent spatial cut-off frequency; however, the difference between the two orientations was less pronounced than the difference between the corresponding interreceptor angles. This led to the assumption that the spiders also react to pure temporal intensity modulations and that, consequently, the angles subtended by one photoreceptor in the two orientations are the limiting factor for the response to moving gratings. A simple simulation of the intensity modulations, taking the photoreceptor geometry into account, suggested that this represents a possible explanation for the reaction of the spiders to horizontal gratings that were actually too fine to be properly resolved by the receptor mosaic (Fenk and Schmid, 2010).

In the present study we tested the assumption that temporal intensity modulations lead to significant responses by recording the muscle activity with a telemetric unit while the spiders were confronted to stimuli presented on a cathode ray tube (CRT) screen. Our assumption was clearly confirmed. The spiders' response to flicker stimuli was then used to estimate the behavioural flicker fusion frequency. The values obtained in our experiments are well in line with the integration time measured by Pirhofer-Walzl et al. in intracellular recordings (Pirhofer-Walzl et al., 2007).

MATERIALS AND METHODS

Animals

We breed *Cupiennius salei* (Keyserling 1877) in a greenhouse where relative humidity (70–80%) and temperature (20–28°C) resemble the conditions in the spiders' natural habitat. The animals are kept separately in 5 l glass jars under a 12 h:12 h day:night cycle and are fed flies (*Calliphora* sp.) once a week. In this study we used 19 adult female spiders. For the experiments, the spiders were cooled down and subsequently tethered onto a turnable wooden spherical cap that was connected to a magnetic stand by means of a ball bearing. The legs, pedipalps and chelicerae were fixed with Parafilm® bands, and the prosoma and opisthosoma were left free. The hairs on the upper part of the prosoma and between the PME were removed before the telemetric unit could be attached to the prosoma using beeswax. The reference electrode was inserted posterio-laterally into the prosoma; the measuring electrode was placed just below a PME. A picture of a tethered spider is shown in Neuhofer et al. (Neuhofer et al., 2009). When a sufficiently good signal-to-noise ratio was achieved, the spiders were positioned at a distance of 20 cm from the screen and rotated approximately 30 deg in the horizontal and vertical planes. All but the PME were covered with red acrylic paint.

Post-ecdysal spider eyes show enlarged pigment rings that diminish while the lens is growing (Fenk et al., 2010a). The pigment supposedly shields light rays that would enter the eye beside the growing lens and might maintain vision in post-ecdysal animals. However, light sensitivity is certainly altered in this state and we thus only used animals that did not show significant rings and could therefore be assumed to have fully developed lenses.

Stimuli

The stimuli were generated in MATLAB (MathWorks, Inc., Natick, MA, USA) using the psychophysics toolbox (Brainard, 1997; Pelli, 1997) and were presented on a CRT monitor (800×600 pixels, 120 Hz; Sony Trinitron Multiscan 300sf, Tokyo, Japan). The monitor was turned on at least 1 h before the experiments started. In the following, flicker frequencies will be given in cycles per second. The flicker stimuli shown in our experiments consisted of periodic changes of light intensity presented in a square at the centre of the screen where, after each half cycle, the square suddenly changes from bright to dark or *vice versa*. Screenshots showing the stimuli used in the two experimental series are shown in supplementary material Fig. S1.

The aim of the first experimental series was to test whether the spiders respond to pure temporal intensity changes. For this purpose, we measured the eye muscle activity while the animals were confronted with bright and dark single-step stimuli and slow flicker. In this series, the whole screen was covered with a stationary checkerboard during inter-stimulus time; the flicker stimuli were shown in a square with a side length of 18.5 cm in the middle of the checkerboard pattern. A checkerboard pattern was chosen as the simplest and most reliable method to match the intensity of the pre-stimulus pattern to the time-averaged intensity of the flickering stimuli. The checkerboard pattern had a wavelength of 1 deg, which is well below the retinal resolution reported for *C. salei* (Land and Barth, 1992), and can therefore be assumed to be not resolved by the spiders. We measured the reaction of seven spiders to the appearance of a dark square, a bright square, flicker starting with a bright square (0.278, 0.554 and 1.11 cycles s^{-1}), flicker starting with a dark square (0.278 cycles s^{-1}) and a counterphase flicker (0.554 cycles s^{-1}). The counterphase flicker was shown to the spiders to test whether responses can also be elicited with stimuli that have an overall intensity that remains constant over time. For this purpose, the square was divided into two vertical halves of opposite brightness that flickered in temporal counterphase. The stimuli were shown for approximately 6.3–7.2 s, depending on the stimulus type; the inter-stimulus time was 50 s. We pooled the first five valid measurements for each spider, i.e. measurements for which the signal-to-noise ratio was sufficient and where no chelicerae movements were registered in the 20 s prior to the stimulus onset or within the first 3 s after stimulus onset. The order in which the different stimuli were shown was different for each spider.

In a second series, we determined the spiders' behavioural flicker fusion frequency. Here only the 18.5×18.5 cm square showed the checkerboard pattern (1 deg wavelength) and the surrounding background was grey. Precise timing was crucial for the correct presentation of high-frequency stimuli and the stimuli were therefore chosen to be as simple as possible. *Cupiennius salei* is known for its excellent mechanosensory systems, and changes in processor load (and thus ventilator noise) could theoretically lead to artefacts. To keep processor load as constant as possible, the checkerboard pattern flickered at the same frequency as the subsequent stimulus. After an inter-stimulus time of approximately 30–34 s, the bright square appeared in place of the checkerboard pattern and started to flicker at a given frequency for 5.6–6.0 s, depending on the flicker frequency. Twelve spiders were shown seven different flicker frequencies ranging between 0.55 and 60 cycles s^{-1}. Again, the order in which the different stimuli were shown was different for each spider. The given sequence of the seven stimuli was repeatedly shown to the spiders (typically six to eight times) until six valid measurements were recorded for each flicker frequency.

The stimuli were shown at the maximal brightness possible with the monitor used. We measured a luminosity of 56.0±0.5 cd m^{-2} for the bright squares, 2.15±0.05 cd m^{-2} for the dark squares and 28.0±0.5 cd m^{-2} for the checkerboard pattern (Luminance Meter, LS-100, Konica Minolta, Tokyo, Japan). The asymmetry, caused by the rendering of the checkerboard on the CRT, was thus in the order of 1 cd m^{-2}. The subsequent slight increase in luminance upon flicker onset was not sufficient to enhance eye muscle activity (see Results for high flicker frequencies). The contrast of the bright and dark square was 0.93.

Telemetry

The activity of the dorsal eye muscles was, as described in previous studies (Neuhofer et al., 2009; Fenk and Schmid, 2010), recorded with a small telemetric unit. The telemetric device proposed by Kutsch et al. (Kutsch et al., 1993) was adapted for spiders in our group. Its main component is an LC-oscillator circuit that generates a carrier frequency of roughly 130 MHz that is frequency and amplitude modulated by the AME muscle potentials. The signal was recorded using a conventional world receiver (Conrad Voyager RY-630, Conrad Electronics, Hirschau, Germany) that was connected to a PC *via* an A/D converter (CED 1401, Cambridge Electronic Design, Cambridge, UK). We registered the muscle's activity for data analysis using Spike2 (Cambridge Electronic Design). This setup is not suitable to measure the absolute amplitude of the muscle potentials; however, this is not needed for our analysis.

Analysis

The eye muscle activity shows great variation and depends on a large number of internal and external factors. The spiders show different resting activities, probably depending on their state of arousal and the activity increases as response to visual stimulation, but also as response to mechanical stimuli (Kaps and Schmid, 1996). We thus averaged several stimulus presentations for each individual spider (five in the first series and six in the second).

To visualize the temporal pattern of the spiders' response, we calculated the mean frequency as a function of time for the 35 presentations of the first experimental series showing slow flicker and the 72 presentations of the second series used to determine the cut-off frequency. For the calculation of the mean temporal patterns, we exported the mean muscle potential frequency for each presentation (as calculated in Spike2 at a bin size of 0.2 s) with an output sample rate of 100 Hz. Subsequently, the arithmetic mean over all trials was calculated for the resulting 100 data points per second.

To determine the highest flicker frequency that elicited a significant increase, we compared the instantaneous muscle potential frequency averaged in the 3 s prior to stimulus onset to the averaged frequency in the 3 s after stimulus onset. Fig. 1 provides an example of the recording of the muscle potentials together with the instantaneous frequency.

The significance of the frequency changes was tested for the spiders using the Wilcoxon signed-rank test in MATLAB (N=7 for the first series, N=12 for the second series).

RESULTS

Single-step stimuli and slow flicker

The spiders responded with a pronounced increase in eye muscle activity to slow flicker, counterphase flicker, as well as step stimuli.

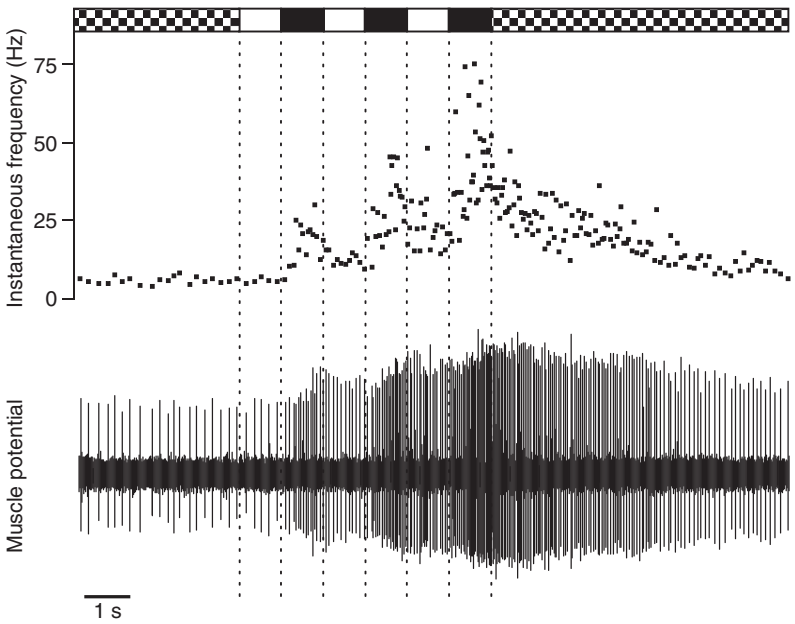

Fig. 1. An example of a single stimulus presentation (0.554 cycles s^{-1}). The first vertical line indicates the change from the checkerboard pattern to a bright square and subsequent lines indicate a change from bright to dark and *vice versa*. We show a response of the spider that had the lowest resting frequency, because here the changes in eye muscle activity are most distinct. The spider did predominantly respond to a decrease in intensity. Our experimental setup is not suited for the measurement of the absolute amplitude of the muscle potentials.

Table 1. Mean (±s.e.m.) changes in *Cupiennius salei* eye muscle activity upon stimulus onset

Stimulus	Change in eye muscle activity (Hz)	*P*
CB to bright (step stimulus)	3.6±1.4	0.0391
CB to dark (step stimulus)	3.0±0.8	0.0078
CB to bright (0.278 cycles s^{-1})	9.3±1.5	0.0078
CB to bright (0.554 cycles s^{-1})	8.9±1.8	0.0078
CB to bright (1.11 cycles s^{-1})	7.5±1.4	0.0078
CB to dark (0.278 cycles s^{-1})	7.1±2.7	0.0234
CB to counterphase (0.554 cycles s^{-1})	4.4±1.1	0.0156

The significance of the activity increases was tested using the Wilcoxon signed-rank test (*N*=7, one-sided value). Stimulus onset is the change from the checkerboard (CB) pattern to a bright or dark square, or to a counterphase flicker. The square either remains bright or dark (step stimulus) or flickers at a given frequency.

Fig. 1 shows the response of the spider with the lowest resting activity, where the rhythmic increase can, as a consequence, be most easily observed. This spider has primarily increased muscle activity upon a decrease in light intensity. The pre-stimulus activity was below 10 Hz and frequency was increased up to 75 Hz for the third change to the dark square.

The mean frequency increase in the first 3 s following the onset of the stimuli compared with the 3 s preceding the stimulus onset ranged between 3.0 and 9.3 Hz. The responses to all seven stimuli were significant (Table 1). Interestingly, the mean increase elicited by the counterphase flicker (4.4±1.1 Hz) was roughly half of the increase elicited by the square of the same size that flickered homogeneously at the same frequency (8.9±1.8 Hz). The mean activity increases as response to the two step stimuli (checkerboard to bright and dark squares) were in the same order of magnitude (3.6±1.4 and 3.0±0.8 Hz, respectively) and step stimuli elicited a significantly lower activity increase than the flicker stimuli at low frequencies.

Fig. 2 shows the temporal pattern of the response to the single-step stimuli and to the lowest presented flicker frequency (0.278 cycles s^{-1}). The curves represent the arithmetic mean of the mean activity (bin size 0.2 s) for the first five stimulus presentations to all spiders (35 presentations). Both the step stimuli and the slow flicker stimuli elicited a mean increase that is steeper for the onset of the dark square than for the bright one. Pooling the response to the step stimulus and the first intensity change of the slowest flicker (0.278 cycles s^{-1}) for the first 0.6 s after stimulus onset, we obtained a slope of approximately 3.0 Hz s^{-1} for the change from the checkerboard pattern to a bright square, and approximately 8.5 Hz s^{-1} for the change to a dark square (R^2>0.95 for both regressions, 70 presentations, 7 spiders, respectively).

Behavioural cut-off frequency

The temporal patterns of the eye muscle activity for three different flicker frequencies are shown in Fig. 3 (mean of all 72 presentations). The first vertical line indicates the change from the checkerboard pattern to a bright square. All subsequent lines indicate a change from bright to dark squares and *vice versa*. The response pattern recorded for the slowest flicker frequency (0.554 cycles s^{-1}) reveals a rhythmic increase in the muscle activity (Fig. 3A). In Fig. 3B, showing the pattern for the highest frequency that elicited a significant response (4.28 cycles s^{-1}), a slight increase upon flicker onset can be seen, with an overall frequency that does not reach the pre-stimulus value in the following 3 s. No distinct peak upon stimulus onset is observed for 8.6 cycles s^{-1}, i.e. the lowest frequency that did not elicit a significant response (Fig. 3C).

The mean frequency changes for the 12 spiders after the onset of the flicker are shown together in Fig. 4. A flicker frequency of 0.554 cycles s^{-1} elicited a mean increase of the spiders' eye muscle activity of 9.5±1.6 Hz. The response of the spiders falls quickly for higher frequencies and the maximal frequency that elicited a significant increase in our experiments was 4.28 cycles s^{-1} (1.1±0.6 Hz; *P*=0.0386, one-sided value). None of the higher frequencies and all of the lower frequencies elicited a significant response. This suggests that the behavioural temporal cut-off frequency lies somewhere between 4.3 and 8.6 cycles s^{-1} for the stimuli used.

DISCUSSION

Our data clearly confirm the hypothesis that *C. salei* responds to pure temporal intensity modulations and that no directed motion is required to elicit an increase in eye muscle activity. The net increase

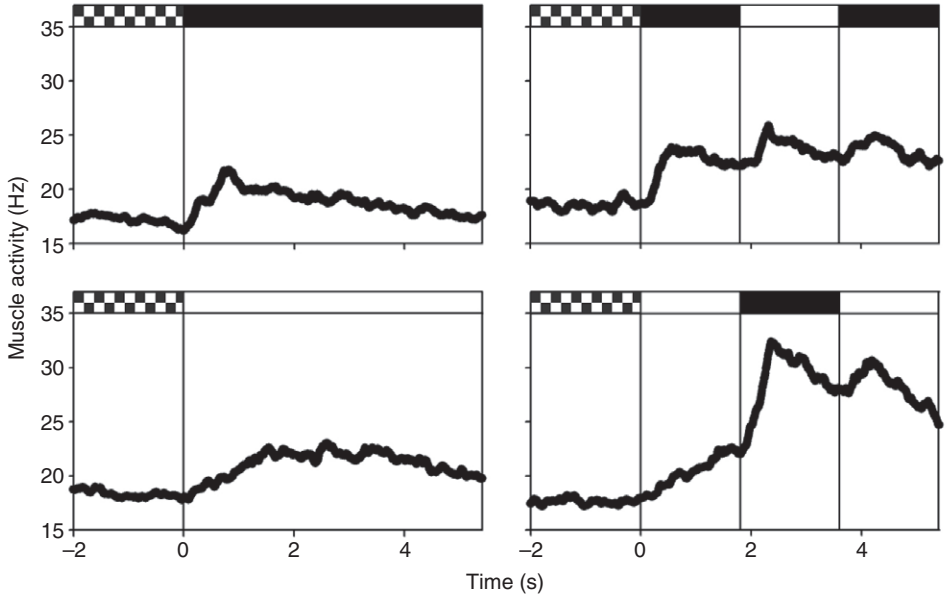

Fig. 2. Mean eye muscle activity of seven *Cupiennius salei* spiders with five presentations each (35 presentations; bin size 0.2 s) for different stimuli as a function of time. The left panels show the averaged response to step changes from the checkerboard pattern to dark (upper) or bright (lower) as indicated at the top of the diagrams. The right panels show the response to the transition from the checkerboard pattern to a flicker (0.278 cycles s^{-1}) starting with a dark (upper) or a bright (lower) square.

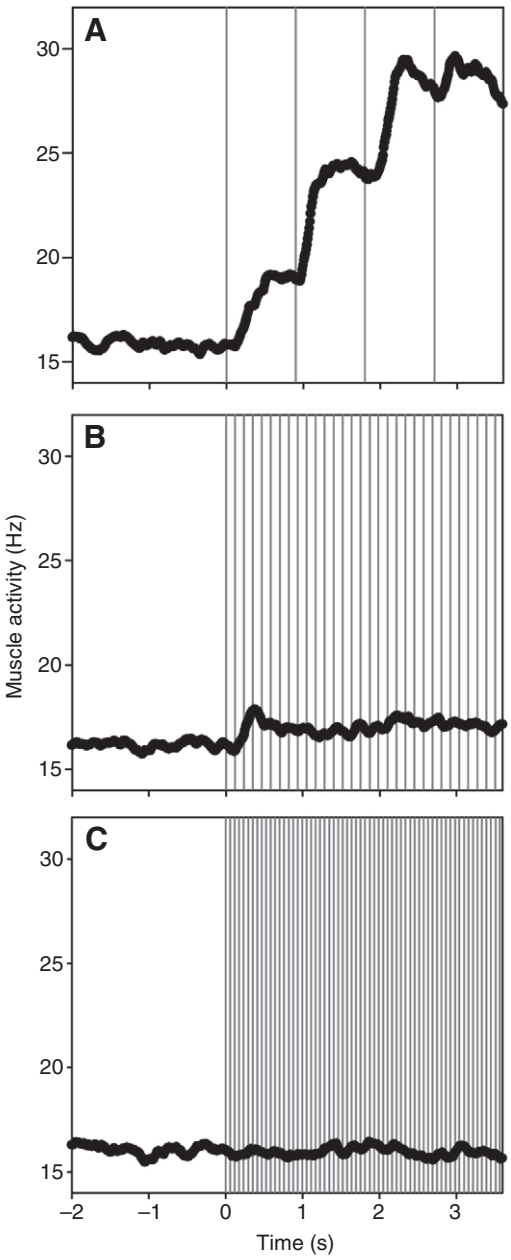

Fig. 3. Mean eye muscle activity (72 stimulus presentations, 12 spiders, bin size: 0.2 s) as response to (A) the slowest flicker of the second series (0.554 cycles s^{-1}), (B) the highest frequency that elicited a significant increase (4.28 cycles s^{-1}) and (C) the lowest frequency that did not elicit a significant increase (8.6 cycles s^{-1}).

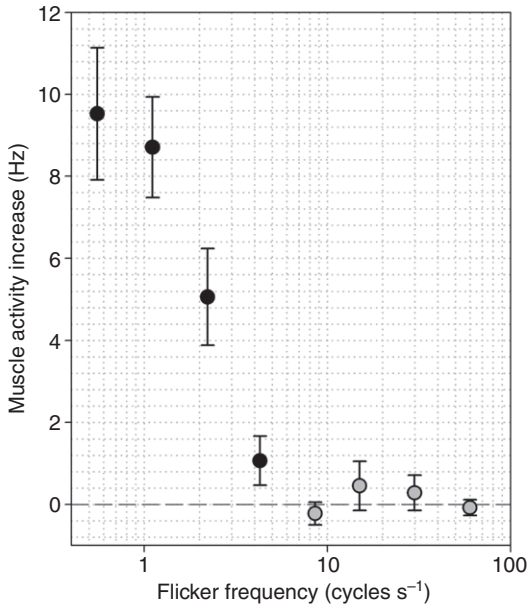

Fig. 4. Mean (±s.e.m.) eye muscle activity increase in the first 3 s after flicker onset compared with the preceding 3 s as a function of flicker frequency for 12 spiders with six presentations each. Black circles give the mean of significant responses (P<0.05, Wilcoxon signed-rank test, N=12, one-sided value); grey circles give the mean of non-significant responses.

in activity of approximately 9 Hz measured for slow flicker frequencies was higher than the increase determined in previous studies for moving stripes (Neuhofer et al., 2009; Fenk and Schmid, 2010; Orlando and Schmid, 2011). The spiders respond reliably, and for sufficiently low flicker frequencies the averaged activity exhibits a rhythmic increase. The slope of the averaged increase was found to be steeper for an intensity decrease than for an intensity increase. This might be compared to the results of a previous study where we showed that the spiders were able to quickly approach visual targets on a computer screen (Fenk et al., 2010b). We found that the spiders were able to follow dark targets on a bright background as well as bright targets on a dark background; however, the attack rate was significantly higher for dark targets. Similar findings are reported for the jumping spider *Menemerus bivittatus*, which was also shown to prefer dark targets on a bright background (Tiedemann, 1993).

Because of the limited brightness of CRT monitors, the present setup does not allow the determination of the spiders' maximum temporal cut-off frequency. The illuminance at the animals' position was 8 lx for the screen showing the dark square and 38 lx for the screen showing the white square. The lower value is very close to the light intensity that elicited a half-maximum response in ERG measurements (Barth et al., 1993) and is more than 4 log units above the spiders' threshold. The light intensity at which spiders leave their retreat at dusk is approximately 20 lx (Barth and Seyfarth, 1979), which is the same order of magnitude as the intensity of the presented stimuli. Our measurements might thus give the order of magnitude of the behavioural cut-off frequency at maximum light intensities encountered by *C. salei* during its active period in the natural environment.

Pirhofer-Walzl et al. (Pirhofer-Walzl et al., 2007) determined the temporal properties of the photoreceptors using intracellular recordings. In dark-adapted PME, the time to peak and the integration time were found to be 142 and 138 ms, respectively; in light-adapted PME these were 87 and 79 ms, respectively (Pirhofer-Walzl et al., 2007). The presentation time of half a cycle for a frequency of 6 cycles s^{-1} (the frequency midway between 4 and 8 cycles s^{-1}) is 83 ms. The image presentation time, i.e. the presentation time of one bright or dark square, thus matches well the magnitude of the integration time of light-adapted PME photoreceptors.

The eye muscle activity increase elicited by flicker is probably a very direct measure of the behavioural cut-off frequency and might thus reflect the highest frequencies that can be detected by

the animals. In these experiments, no directional information has to be taken into account by the animals, in contrast to studies based on optomotor response or prey capture (e.g. Autrum and Stoecker, 1950; Autrum, 1952; Haldin et al., 2009) where the animals have to compute the direction of moving stimuli. Nor are the animals required to learn, as is the case in studies based on discrimination tasks (e.g. Srinivasan and Lehrer, 1984a; Srinivasan and Lehrer, 1984b; Railton et al., 2009). The performance of animals might differ considerably according to the behavioural tasks investigated. Autrum and Stoecker showed that optomotor response in honeybees persists up to 200 Hz (Autrum and Stoecker, 1950). In discrimination tasks, however, bees seem to be almost unable to use monochromatic temporal intensity modulations (Lehrer et al., 1993).

It might be interesting to compare *C. salei* with the toad, a well-studied vertebrate with a similar lifestyle (see Pirhofer-Walzl et al., 2007). Both animals are nocturnal predators that remain motionless waiting for prey to pass by. The neural images in the toads' eyes and the spiders' motionless secondary eyes are assumed to adapt to stationary surroundings, and only moving objects would pop up on the animals' retinae (Ewert and Borchers, 1974; Land and Barth, 1992). Toad rod photoreceptor cells have integration times of 1.0–1.3 s at 25°C, and substantially longer integration times at lower temperatures (Haldin et al., 2009) and are thus roughly 10 times slower than photoreceptors in *C. salei*. A good match was found between the integration time of the toad rod photoreceptor cells at different temperatures and the 'exposure time' of a dummy necessary to elicit prey capture (Haldin et al., 2009).

The orientation-dependent spatial cut-off frequencies (Fenk and Schmid, 2010) and the different interreceptor angles (Land and Barth, 1992) suggest that object detection and localization should be best in the spiders' frontal plane. The photoreceptor cells subtend smaller angles along the tapetal rows parallel to the spiders' frontal plane than normal to it. The elongated photoreceptor cells might allow increased photon capture, and thus increased signal-to-noise ratio in the spiders' dim environment, while maintaining relatively precise spatial information about an object's position in the spider's principal plane of action. The behavioural temporal cut-off frequency of a few cycles per second and the spatial cut-off frequency of 0.5 cycles deg^{-1} suggest that *C. salei* sacrifices temporal rather than spatial resolution to increase sensitivity. Relatively large integration times and relatively good spatial acuity is what one would predict for sedentary animals interested in small, slowly moving objects (Warrant, 1999). This suits perfectly *C. salei*'s lifestyle as a typical sit-and-wait hunter, living in a dim habitat, that also uses visual cues during prey capture.

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